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Parental effects on offspring life histories: when are they important?

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Both the parental legacy and current environmental conditions can affect offspring life histories; however, their relative importance and the potential relationship between these two influences have rarely been investigated. We tested for the interacting effects of parental and juvenile environments on the early life history of the marine fish *Acanthochromis polyacanthus*. Juveniles from parents in good condition were longer and heavier at hatching than juveniles from parents in poor condition. Parental effects on juvenile size were evident up to 29 days post-hatching, but disappeared by 50 days. Offspring from good condition parents had higher early survival than offspring from poor-condition parents when reared in a low-food environment. By contrast, parental condition did not affect juvenile survival in the high-food environment. These results suggest that parental effects on offspring performance are most important when poor environmental conditions are encountered by juveniles. Furthermore, parental effects observed at hatching may often be moderated by compensatory mechanisms when environmental conditions are good.

Keywords: coral reef fish; environmental variability; food availability; parental effects; compensatory mechanisms; intergenerational interactions

1. INTRODUCTION

Parents can influence the phenotype and life-history traits of their progeny through both genetic and non-genetic means (Kirkpatrick & Lande 1989). Variations in the environmental conditions experienced by parents may affect their physiological condition and provide the opportunity for non-genetic effects to be transferred to their offspring. Generally, larger or better conditioned parents tend to produce larger offspring (Einum & Fleming 1999). In some species, a larger initial body size is correlated with a faster growth rate (Marshall *et al.* 2006) and these individuals more rapidly attain size thresholds required to escape high levels of predation (Ellis & Gibson 1995). Individuals that are initially larger than others may be able to maintain this size advantage to important life-history events, such as maturity and reproduction (Altmann & Alberts 2005; Le Galliard *et al.* 2005). Despite the widespread occurrence of non-genetic parental effects, their relative importance for the ecology of species compared to other environmental influences has rarely been assessed.

The environment experienced by juveniles can also have substantial effects on phenotypes (West-Eberhard 2003) and life histories (Stearns 1992). Across a wide range of taxa, the environmental conditions experienced by juveniles can directly affect growth rate and survival (Altmann & Alberts 2005; Le Galliard *et al.* 2005; McCormick & Meekan 2007). In general, high-quality food environments tend to yield larger individuals with increased survival compared with low-quality food environments (Altmann & Alberts 2005). Thus, the relative importance of parental effects will depend on their magnitude compared to the effect that current environment has on offspring growth and survival (Bize *et al.* 2002). Parental effects may be trivial if environmental conditions in the offspring's generation have a far greater effect on individual performance, or if initial differences in size or condition are rapidly moderated by compensatory mechanisms in juveniles (Rombough 1994).

Beneficial parental influences are expected to be most important when offspring experience poor environmental conditions, and there is some evidence to support this hypothesis (Marshall *et al.* 2006; Bonduriansky & Head 2007). For most species, however, the potentially complex relationships between parental effects and the juvenile environment are unknown. We experimentally tested the interacting effects of differences in food supply during both the parental and juvenile stages on the growth and survival of a tropical damselfish, *Acanthochromis polyacanthus*. Using an orthogonal design, where breeding pairs were fed either a low- or a high-quantity diet and their offspring were reared on either a low- or a high-quantity diet, the relative importance of parental effects on the growth and survival of offspring under different environmental conditions was assessed.

2. MATERIAL AND METHODS

(a) *Study species and adult rearing conditions*

A. polyacanthus is a pair-forming fish that broods its young for up to 45 days after hatching (Kavanagh 2000). Eleven adult pairs were collected around Orpheus Island on the Great Barrier Reef (Australia) and housed in 70 l aquariums with a constant flow of seawater at a rate of 2.5–3 l min^{-1}. Pairs laid egg clutches of 450–700 eggs on the underside of a terracotta (Donelson *et al.* 2008). Adults were fed a combination of commercial fish flakes and pellets in either high-quantity (six pairs) or low-quantity diet (five pairs). The high-quantity diet was exactly three times the low-quantity diet. After 6 weeks on the different diets, and prior to breeding, adult fish on the high-quantity diet were in significantly better body condition, having a greater weight for a given length, than adult fish on the low-quantity diet (ANCOVA: $F_{1,19}=10.60$, $p=0.004$; see Donelson *et al.* (2008) for details).

(b) *Offspring characteristics at hatching and 7 days post-hatching*

On the day of hatching, 20 juveniles from each clutch were haphazardly selected for measurement of weight (nearest mg) and standard length (SL) (nearest 0.01 mm). The remaining juveniles were fed daily with newly hatched *Artemia* nauplii at a rate of 2 nauplii ml^{-1} of the parental tank. Another 20 juveniles were sampled 7 days after hatching. SL was estimated by computer image analysis (Image Tool, UTHSCSA, San Antonio, TX, USA) of fish photographed under a stereomicroscope.

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(c) *Juvenile rearing conditions*
To test for the interacting effects of the current environment and the parental condition on the growth and survival of offspring, juveniles from parents in each food treatment were reared on either a high- or a low-quantity diet. Forty juveniles from each of five high-food parents and four low-food parents were haphazardly selected at 7 days post-hatching and transferred to individual 2 l aquariums supplied with a constant flow of seawater at a temperature of 28.3±0.4°C. Twenty juveniles from each group were fed *Artemia* nauplii at a concentration of one individual ml^{-1} day (high-food treatment). The other 20 juveniles were fed the same ration every third day (low-food treatment). From day 12 onwards, juveniles were also fed approximately 3 mg of INVE Aquaculture Nutrition 2/4 NRD pellets per day (high-food treatment) or every third day (low-food treatment). Aquaria were checked daily at 09.00 and deaths within the past 24 hours recorded. Half of the individuals alive were sampled at day 22 of the experiment (29 days post-hatching) and the remaining individuals were sampled at day 43 (50 days post-hatching). Each fish was measured (SL) and weighed.

(d) *Data analysis*
ANOVA was used to compare the size (SL and weight) of offspring produced by adults on high- and low-quantity diets on the day of hatching and 7 days post-hatching. Mann–Whitney *U*-tests were used where ANOVA assumptions were not met. Two-way ANOVA was used to compare the growth (SL and weight) of offspring in the two different juvenile food treatments, depending on adult feeding treatments. Two sample survival analysis (Gehan's Wilcoxon test) was used to compare the mortality patterns within and between the juvenile feeding levels.

3. RESULTS

(a) *Growth*
Offspring from high-food parents were 6 per cent larger and 21 per cent heavier at hatching compared with offspring from low-food parents (mean SL: 5.59 versus 5.27 mm; $U=1602$, $p<0.001$, $n=180$; mean weight: 3.77 versus 2.98 mg; $F_{1,178}=7.07$, $p<0.001$). At 7 days post-hatching, offspring from high-food parents were 8 per cent larger and 25 per cent heavier than offspring from low-food parents (mean SL: 8.142 versus 7.497 mm; $F_{1,178}=38.6$, $p<0.001$; mean weight: 11.19 versus 8.95 mg; $F_{1,178}=38.08$, $p<0.001$).

Growth of juvenile fish was strongly influenced by food availability (figure 1). Juveniles in the high-food treatment were significantly longer and heavier than those in the low-food treatment at 29 and 50 days post-hatching (table 1). The difference in length between the food treatments was substantial, with juveniles in the high-food treatment being over 35 per cent longer at 29 days, and 60 per cent longer at 50 days, than those from the low-food treatment. Despite the rapid growth of juveniles, differences in length and weight of offspring as a result of differences in parental diet were still evident 29 days post-hatching (table 1; figure 1). However, these differences had disappeared by 50 days post-hatching (table 1; figure 1).

(b) *Survival*
Close to 100 per cent survival occurred in the high-food treatment (figure 2*a*). By contrast, mortality was over 70 per cent in the low-food treatment (figure 2*b*). Parental diet did not affect offspring survival in the high-food treatment ($z=1.63$, $p>0.05$; figure 2*a*), but had a significant effect in the low-food treatment ($z=2.79$, $p<0.05$; figure 2*b*). In the period from 15 to 25 days post-hatching, 30 per cent more

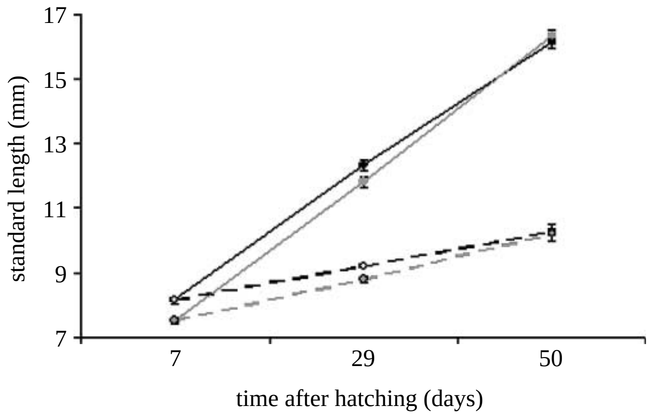

Figure 1. Mean growth (±s.e.) of *A. polyacanthus* juveniles on high (solid lines) and low (dashed lines) quantity diets, and in relation to the feeding regime of their parents on high (black circles) or low (white circles) food diet.

offspring survived from parents fed a high-food diet (figure 2*b*). However, by 27 days post-hatching, the number of surviving offspring did not differ between the adult food treatments.

4. DISCUSSION

The importance of non-genetic parental effects on offspring attributes depended on the specific life-history trait examined. The effect of parental body condition on juvenile size lasted for more than 29 days post-hatching regardless of juvenile diet. By contrast, parental effects influenced the survival of juveniles in the low-food treatment, but had no effect in the high-food treatment. This demonstrates that the importance of parental history on the fitness of offspring can be highly dependent on the environmental conditions that juveniles experience and is likely to be most important when offspring encounter unfavourable or stressful conditions.

We found that the differences in size at hatching were maintained for over four weeks, which has potentially important implications for offspring fitness. Many reef fishes suffer exceptionally high mortality rates during early life (Almany & Webster 2006), which can be selective for size (McCormick & Meekan 2007) or body condition (Hoey & McCormick 2004). Consequently, smaller offspring from parents in poor condition are likely to be exposed to high mortality rates for a longer period of time compared with the larger offspring from parents in good condition. However, we also found that offspring from parents in poor condition exhibited compensatory growth. This indicates that non-genetic parental effects do not permanently limit the offspring's phenotype. Compensatory growth has been identified in a range of taxa (e.g. Nicieza & Metcalfe 1997; Gagliano & McCormick 2007) and may be an important mechanism for overcoming unfavourable size-based selection during the early life history. However, growth compensation is also known to produce subsequent costs to the individual (Arendt *et al.* 2001), which may offset the advantages of compensatory growth in the long

Table 1. Comparison of the weight of offspring between adult feeding treatments (adult food) and juvenile feeding treatments (juv. food). (Italics indicate significant p-values.)

	day 29		day 50	
	SL	weight	SL	weight
adult food	$F_{1,110}=5.57$	$F_{1,110}=8.89$	$F_{1,88}=0.554$	$F_{1,88}=0.017$
	p=0.02	*p=0.004*	$p=0.459$	$p=0.895$
juv. food	$F_{1,110}=232.66$	$F_{1,110}=406.85$	$F_{1,88}=277.76$	$F_{1,88}=333.10$
	p<0.001	*p<0.001*	*p<0.001*	*p<0.001*
adult × juv. food	$F_{1,110}=0.204$	$F_{1,110}=1.01$	$F_{1,88}=2.03$	$F_{1,88}=0.47$
	$p=0.652$	$p=0.318$	$p=0.158$	$p=0.495$

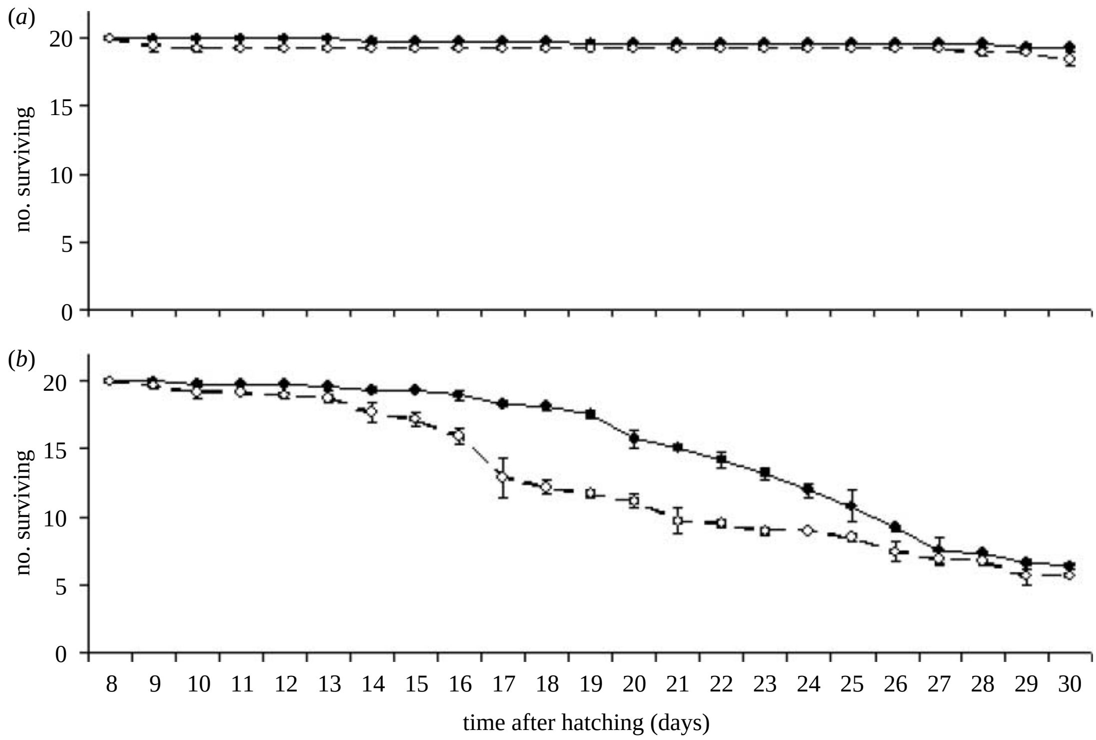

Figure 2. Mean survival (±s.e.) of *A. polyacanthus* offspring produced by parents consuming high (filled circles) and low (open circles) food diets in (*a*) juvenile in high-food environments and (*b*) juvenile in low-food environments.

term. The high early mortality of offspring from poor-condition parents is possibly a cost of the compensatory growth exhibited.

Juvenile environment had a major influence on young *A. polyacanthus*, with high-food availability producing significantly higher growth. The relative difference in size due to juvenile environment was substantially greater than that caused by parental condition. This suggests that the importance of parental effects can only be properly understood in the context of the environmental conditions experienced by the offspring. Small size differences between juveniles owing to parental effects may only be emphasized in a competitive social setting where larger individuals gain proportionally more resources than their smaller counterparts (Marshall *et al.* 2006). Juveniles for which parental care is provided during early life are often more greatly influenced by this care than original provisioning (Bize *et al.* 2002). However, this does not show a direct relationship between the current juvenile environment and the parental effects because environmental effects are mediated through parents, allowing the parental phenotype to still have an influence.

Importantly, we found that a combination of parental condition and juvenile food availability influenced the survival of *A. polyacanthus* juveniles. Offspring from poor-condition parents had a period of increased mortality when reared in the low-food environment. While there was similar survival of juveniles after 27 days post-hatching, possibly because beneficial parental effects are not everlasting, the first weeks of life on the reef are known to be critical to individual success (McCormick & Hoey 2004; Almany & Webster 2006). Therefore, it is likely that this period of differential survival, as well as the reduced size at hatching, may combine to cause juveniles from poor-condition parents to be strongly disadvantaged when exposed to unfavourable environmental conditions.

The combined effects of parent condition and the current environment on offspring survival could have long-term population consequences. A period of differential survival when conditions are poor would mean that the offspring from good-condition parents will tend to make a much greater contribution to the future population. Conversely, slow-growing genotypes may be retained in the population if good conditions for offspring occur with sufficient frequency. These results may help explain why suboptimal genotypes often remain within populations.

To fully understand the importance of parental effects, we need to consider them in relation to the conditions that offspring experience. The environment is spatially and temporally heterogeneous and the conditions offspring experience may differ from those of their parents. Our results indicate that parental effects can influence mortality schedules of juveniles with a lasting effect on population replenishment and population genetic structure, but these effects are likely to be more pronounced in low-quality habitats or during periods of increased environmental stress.

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